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# EVOLUTION OF BREEDING SYSTEMS IN *EICHHORNIA* (PONTEDERIACEAE): A REVIEW<sup>1</sup>

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## ABSTRACT

*Eichhornia* is of New World origin and comprises eight species of freshwater aquatics in the monocotyledonous family Pontederiaceae. *Eichhornia* flowers display a broad range of morphological specializations associated with their pollination mechanisms and breeding systems. These range from large-flowered, outcrossing, tristylous populations to small-flowered, predominantly self-fertilizing, semi-homostylous populations. Two sources of evidence indicate that the major pathway of breeding system evolution in the genus involves the repeated breakdown of tristily to give rise to selfing semi-homostylous populations: the occurrence of semi-homostylous forms in each of the primarily tristylous species (*E. azurea*, *E. crassipes*, *E. paniculata*) and the presence of residual heteromorphisms, associated with the tristylous syndrome, in the largely autogamous semihomostylous species (*E. diversifolia*, *E. heterosperma*, *E. paradoxa*). It is suggested that genetic bottlenecks associated with long-distance dispersal and colonization of aquatic habitats with uncertain moisture regimes play major roles in disrupting the maintenance of tristily. This leads to the breakdown of the polymorphism and the evolution of semi-homostyly.

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*Eichhornia* (Pontederiaceae) is a small genus comprised of eight species of freshwater aquatics and palustrial herbs. All species, with the exception of the exclusively African *E. natans*, are native to the New World tropics. *Eichhornia azurea* and *E. paniculata* are used as pond ornamentals, and *E. crassipes* (water hyacinth) has spread, with man's aid, from lowland tropical South America to become one of the world's most noxious aquatic weeds.

The flowers of *Eichhornia* are usually mauve-blue and showy, and are pollinated primarily by bees and butterflies. They display a broad range of morphological specializations associated with their pollination mechanisms and breeding systems. The variation ranges from large multicolored tristylous flowers adapted to outcrossing to small uniformly colored self-fertilizing homostylous flowers. This diversity provides suitable experimental material for studies of breeding system evolution. The present review summarizes work on this topic with special attention to the evolutionary breakdown of tristily and the responsible ecological and genetic factors.

Heterostyly is a genetically controlled floral polymorphism in which plant populations contain two (distyly) or three (tristyly) morphs that differ primarily in style and stamen length, pollen size,

and incompatibility behavior. The polymorphism promotes disassortative mating between the floral morphs and is reliably reported from 24 angiosperm families of which just three (Lythraceae, Oxalidaceae, Pontederiaceae) contain tristylous members (Ganders, 1979). A common feature of heterostylous breeding systems is their propensity to become evolutionarily modified in the direction of increased self-fertilization. The main pathway is by the formation of self-compatible homostyles. Plants in these groups possess anthers and stigmas at the same level within a flower and, as a result, are largely autogamous. In tristylous species homostyles often have only one of their two anther sets adjacent to the stigma and as a result are referred to as semi-homostylous (Stout, 1925; Ornduff, 1972). The breakdown of heterostyly to homostyly represents a paradigm for studies of the evolution of self-fertilization in plants, because the direction of change is readily interpretable, genetic modifications are often simply inherited, and alterations in the floral polymorphisms that influence mating behavior can usually be detected without difficulty under field conditions (Barrett, 1988a).

We have investigated the pathways and mechanisms of breeding system evolution in *Eichhornia*

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by adopting the comparative approach employed by many plant systematists and evolutionists (e.g., Stebbins, 1957; Baker, 1966; Grant & Grant, 1965; Lloyd, 1965; Moore & Lewis, 1965; Raven, 1979). Here the working hypothesis is that among closely related taxa of outcrossers and selfers the former condition is usually ancestral and the latter derived. Stebbins (1974) has argued that this pathway has been followed by more lines of evolution in the flowering plants than has any other.

To test this hypothesis in *Eichhornia* two types of evidence were sought. Population studies of outcrossing taxa were conducted to establish whether, under present conditions, the shift from outcrossing to selfing is occurring. Of primary importance in these studies is to determine whether genetically based differences in mating patterns occur both within and between populations of the tristylous taxa. A second line of enquiry has involved interspecific studies of the floral biology of selfing taxa to discover whether residual tristylous traits are evident (see Crowe, 1964). Their occurrence can be taken as evidence of descent from tristylous ancestors, unless we are prepared to accept that tristily is in *statu nascendi* within different selfing lineages of the genus. Given the rarity of the polymorphism in the angiosperms as a whole, this evolutionary scenario seems unlikely (see Eckenwalder & Barrett, 1986).

This review summarizes evidence in favor of the derived nature of selfing taxa and evaluates several hypotheses concerned with the selective mechanisms responsible for the breakdown of tristily. Before this is done, however, a brief summary of the systematic and ecological characteristics of the genus is required.

#### SYSTEMATICS AND ECOLOGY

*Taxonomy.* Most floristic works and regional floras follow Solms-Laubach (1883) and Schwartz (1927, 1930) in their treatments of *Eichhornia* (e.g., Alexander, 1937; Schulz, 1942; Castellanos, 1958; Agostini, 1974; Rosatti, 1987). Schwartz recognized two sections in the genus, the primitive *Protoeichhornia* composed of *E. paniculata* and *E. paradoxa*, and the more advanced *Eichhornia* ("Eueichhornia") containing *E. azurea*, *E. crassipes*, *E. natans*, and *E. diversifolia*. More recently, two frequently overlooked species, *E. heterosperma* and *E. meyeri*, have come to be recognized. *Eichhornia heterosperma*, first described in 1939 from Venezuela by Alexander (Smith, 1939) and very similar in vegetative traits to *E. azurea*, is widely distributed in Central and

South America and is misidentified in most collections (Horn, 1987). Similarly, *E. meyeri* has most often been treated as a synonym of *E. paniculata*, which it resembles closely. It is known from a few localities in Paraguay and from the type locality in the Chaco of Argentina (Schulz, 1942).

*Phylogeny.* A recent cladistic analysis of the Pontederiaceae by Eckenwalder & Barrett (1986) is of interest because most cladograms produced were in conflict with Schwartz's sectional treatment of *Eichhornia* and the genus was paraphyletic under most methods of cladogram construction. Of particular relevance to breeding system evolution was the placement of tristylous and homostylous taxa. Two contrasting patterns emerged from the analyses, neither of which is supported by microevolutionary studies presented below. Most cladograms separated homostylous species of *Eichhornia* as a clade not closely associated with tristylous *Eichhornia* and *Pontederia* but allied instead to *Heteranthera*. This seems unacceptable because of the clear relationships among species such as *E. azurea* (tristylous) and *E. heterosperma* (homostylous), and *E. paniculata* (tristylous) and *E. meyeri* (homostylous). A second pattern derived homostylous taxa from tristylous ancestors, but in this case all homostylous taxa were united as a monophyletic group implying a single origin for homostyly. However, evidence presented below indicates that tristily has broken down repeatedly within *Eichhornia*, implying multiple origins for homostyly in the genus. These disparities probably result from the choice of characters used in cladogram construction. The parallel evolution of the selfing syndrome in different homostylous taxa may provide enough characters to unite species during tree construction. This difficulty has been recently discussed at length by Wyatt (1988) in his review of phylogenetic aspects of the evolution of self-pollination.

*Genetic systems.* Breeding systems and chromosome numbers of *Eichhornia* species are given in Table 1. Three of the eight species are primarily tristylous, and the remaining five are semi-homostylous. However, because of considerable intraspecific variation in floral traits, it is important to note that these terms refer to the most common condition within each species. In *Eichhornia* polyploidy and aneuploidy are derived from an original base number of  $x = 8$ . Unlike other heterostylous groups (e.g., *Turnera ulmifolia* L., Barrett & Shore, 1987), there is no evidence of an association between breeding system and ploidal level. Tristily and semi-homostyly occur at the diploid and tetraploid level.

TABLE 1. Genetic systems, life forms, and distributions of *Eichhornia* species. Breeding systems indicated are the most common condition within each species.

Taxon	Major Breeding System	Chromosome Number ( <i>n</i> )	Life Form	Clonal Propagation	Native Distribution
<i>E. azurea</i> (Swartz) Kunth	tristylous	16	floating-leaved aquatic, long-lived perennial	++	widespread, Neotropics
<i>E. crassipes</i> (Mart.) Solms-Laub.	tristylous	16	free-floating aquatic, long-lived perennial	+++	widespread, lowland South America
<i>E. paniculata</i> (Spreng.) Solms-Laub.	tristylous	8	emergent aquatic, short-lived perennial or annual	—	locally abundant, northeast Brazil, Cuba, Jamaica, Nicaragua, Ecuador
<i>E. heterosperma</i> Alex.	semi-homostylous	15	floating-leaved aquatic, perennial	++	widespread, Neotropics
<i>E. diversifolia</i> (Vahl) Urb.	semi-homostylous	15	floating-leaved aquatic, perennial or annual	+	widespread, Neotropics
<i>E. natans</i> (Beauv.) Solms-Laub.	semi-homostylous?	—	floating-leaved aquatic, perennial or annual	+	widespread, Africa
<i>E. paradoxa</i> (Mart.) Solms-Laub.	semi-homostylous	8	emergent aquatic, annual	—	rare, Guatemala, Venezuela, Brazil
<i>E. meyeri</i> Schulz	semi-homostylous?	8	emergent aquatic, annual	—	rare, Paraguay, Argentina

*Distribution.* The three diploids of *Eichhornia* have narrower distributions than the tetraploids (Table 1) have. In particular, *E. paradoxa* and *E. meyeri* are rare with relatively few known localities. The distribution patterns of the three diploids support Schwartz's (1927) view that the species are phylogenetically old and that their current distributions may represent relict areas of previously wider ranges. The remaining New World *Eichhornia* species all have widespread distributions throughout lowland South America, Central America, and parts of the Caribbean. Unlike the diploids, which are annual or short-lived perennial emergent aquatics with no clonal propagation, all tetraploids exhibit extensive lateral growth either through a branching internode system or by stolons. Fragmentation facilitates clonal regeneration, and all tetraploid species, particularly *E. crassipes*, are capable of prolific vegetative spread. The ability to disperse by seeds and floating vegetative fragments may contribute to the wider distributions of tetraploid than diploid taxa.

The Pontederiaceae are of New World origin with all but one species of *Eichhornia* native to the Neotropics. The African *Eichhornia natans* is likely descended from New World ancestors following long-distance dispersal. Its homostylous

breeding system would favor establishment and subsequent spread in Africa following long-distance dispersal from the New World. The most likely progenitor of *E. natans* is *E. diversifolia*, which is very similar in appearance and has been considered conspecific by some taxonomists. The small seeds of *Eichhornia* species and their occurrence in habitats frequented by migratory water birds provide opportunities for long-distance dispersal. This may account for the disjunct and scattered distributions of many of the species.

*Ecology and life history.* There have been no detailed ecological studies of the life history, demography, or habitat preferences of *Eichhornia* species in their native ranges. The following field observations, while rudimentary, may stimulate more in-depth work as well as providing the necessary ecological background from which to discuss the reproductive biology and evolution of breeding systems in the genus.

*Eichhornia* species are exclusively freshwater aquatics. They occupy a diversity of wetland habitats ranging from large water bodies, such as major river systems, lakes, and reservoirs, to extensive marshlands, seasonal pools, and low-lying pastures. Several species are also capable of colonizing sites

disturbed by man, such as rice fields, irrigation canals, and drainage ditches. It is not uncommon to find two or three species of *Eichhornia* at the same site. Significant features of aquatic habitats that determine the presence of individual taxa appear to be permanency of the habitat, water level fluctuations, and overall water depth. These factors not only influence the type of regeneration strategy employed by *Eichhornia* species, but also the composition of the aquatic community and hence the degree of interspecific competition.

*Eichhornia azurea* is a large, long-lived, mat-forming perennial which most commonly occurs in permanent water bodies such as rivers, lakes, and extensive marshlands. The long duration of its pre-reproductive phase restricts the species from colonizing habitats subject to seasonal desiccation. The mat-forming *Eichhornia crassipes* possesses a similar ecology, although it is capable of reaching reproductive maturity more rapidly (Barrett, 1980a) and is often found in more seasonal environments. Unlike *E. azurea*, which is a rooted, floating-leaved aquatic, the free-floating *E. crassipes* is able to colonize environments that experience large fluctuations in water level (Barrett, 1977a, 1979). *Eichhornia heterosperma* commonly occurs in shallow lakes and ponds. Its abundance in the highly seasonal environments of the Llanos of Venezuela and in the caatinga of northeast Brazil indicates that it is capable of withstanding habitat desiccation, presumably as rhizomes or seed. *Eichhornia paniculata* occurs in seasonal pools, rice fields, and low-lying pastures. In comparison with the preceding species, it is capable of colonizing more terrestrial environments that experience only limited periods of inundation. The life history of *E. paniculata* depends largely on available moisture. When available for extended periods, plants perennate; however, at many locations in northeast Brazil and in Jamaica, populations are annual and regenerate from seed (Barrett, 1985a). An annual life history is also implicated for *E. meyeri* in the seasonal environment of the Chaco of Argentina (Schulz, 1942).

Owing to the rarity of *E. paradoxa*, little is known of its ecology. I have observed two populations in northeast Brazil. At one site in Paraiba state the species was growing in a roadside depression with *E. paniculata*; at the other location it occupied a low-lying floodplain of the São Francisco River. These observations suggest that the species prefers seasonally inundated sites.

*Eichhornia diversifolia* is most commonly found in seasonal ponds that experience large water-level fluctuations. During the vegetative growth period it is often in water 1–2 m deep, and as the water

level drops, plants flower and mature seed. The species usually behaves as an annual and may require water-level fluctuations for successful seed germination and establishment. *Eichhornia diversifolia* colonizes rice fields and can be considered a fugitive species adapted to temporary aquatic environments. Habitat descriptions on herbarium specimens and flora accounts of *E. natans* in Africa suggest a similar ecology. The species is reported as a rice field weed in Nigeria (Vaillant, 1967).

*Reproductive biology.* The contrasting breeding systems and life histories of *Eichhornia* species are associated with diverse reproductive attributes (Table 2). In general, the outcrossing species possess large showy flowers, inflorescences with many flowers, high pollen-ovule ratios, and heavier seeds in comparison with selfing species. It is important to emphasize that each *Eichhornia* species shows considerable variation in reproductive traits. The values presented in Table 2 are from a single population of each species and were chosen to illustrate overall trends in reproductive traits among species. With the exception of data presented for *E. meyeri*, all values are based on field-grown plants. Exceptions to the trends discussed above are apparent, however, such as in *E. paniculata*, where individual flowers are similar in size to several of the selfing taxa. Inflorescences of this species contain many more flowers (up to 300) than other *Eichhornia* species so that the overall floral display of plants is by no means diminished because of their smaller flowers. Figure 1 illustrates the dramatic difference in floral display of tristylous *E. crassipes* and semi-homostylous *E. paradoxa*.

#### TRISTYLY IN THE PONTEDERIACEAE

*The tristylous syndrome.* To understand the evolutionary modifications of tristylous in the Pontederiaceae it is necessary to describe the morphological, physiological, and functional aspects of trimorphic incompatibility. Populations of tristylous plants are composed of three floral morphs known as the long-, mid-, and short-styled morphs (hereafter referred to as L, M, S). Each plant possesses flowers with two anther levels that correspond to the stigma levels in the remaining two morphs. Thus, as illustrated in Figure 2, there is a reciprocal positioning of anthers and stigmas in the three floral morphs. Pollinations between anthers and stigmas of equivalent height result in seed set and are termed “legitimate” following Darwin (1877). The remaining pollinations are referred to as “illegitimate” and result in little or no seed set.

A unique feature of tristylous plants is the pro-

TABLE 2. *Reproductive attributes of New World species of Eichhornia. Values are the mean for a representative population sample of each species sampled from the native range. Eichhornia meyeri glasshouse-grown plants.*

Taxon	Flower Breadth (in mm)	Number of Flowers per Inflorescence	Ovule Number per Flower	Pollen-Ovule Ratio	Seed Weight (mg)
<i>E. azurea</i>	44.0	46.2	169.7	204.0	1.062
<i>E. crassipes</i>	58.2	17.2	150.0	255.2	0.297
<i>E. paniculata</i>	24.0	82.0	109.7	192.2	0.147
<i>E. heterosperma</i>	16.1	6.8	134.0	60.7	1.104
<i>E. diversifolia</i>	20.6	3.8	225.5	43.2	0.074
<i>E. paradoxa</i>	17.6	2.0	172.8	37.9	0.083
<i>E. meyeri</i>	16.9	26.0	273.1	18.8	0.281

duction, by the two anther levels within a flower, of distinct pollen phenotypes that differ in their size and incompatibility behavior. Associated with pollen heteromorphism are differences in the amount of pollen produced by the three stamen levels. Long-level anthers produce small numbers of large-sized pollen grains; mid-level anthers produce intermediate amounts of mid-sized pollen grains; and short-sized anthers produce large numbers of small-sized pollen grains. Several other floral polymorphisms often accompany the stamen-style trimorphism (e.g., stigmatic papillae length, style coloration, pollen exine sculpturing). These traits often vary among taxa in their occurrence and expression.

Genetic studies of the inheritance of tristylly in the three tristylous families indicate that the most common mode of control is by two diallelic loci (*S*, *M*) with *S* epistatic to *M* (Fig. 2). With this genetic control and legitimate mating among the morphs, an isoplethic equilibrium (1:1:1) is the only possible condition in large populations, provided that the morphs are of equal fitness (Fisher, 1941, 1944; Heuch, 1979). This expectation provides a "standard" for a fully functional tristylous system, and surveys of style morph frequencies in natural populations can be viewed as the logical starting point for studies directed toward understanding the causes of modification in tristylous systems.

In no species of *Eichhornia* or *Pontederia*, the two tristylous genera of Pontederiaceae, does the expression of tristylly conform to all of the features described above. The tristylous syndrome of *Pontederia* most closely resembles this hypothetical state with the major departure involving the self-incompatibility system. In the four taxa of *Pontederia* that have been examined experimentally the M morph is moderately self-compatible when pollinated with pollen from long-level anthers, whereas incompatibility expression in the L and S morphs is considerably stronger (Ornduff, 1966;

Barrett, 1977b; Glover & Barrett, 1983; Barrett & Anderson, 1985). The significance of this variation to the functioning of tristylly is unclear, since it is not associated with modifications in the stamen-style polymorphism or features of pollen trimorphism.

While trimorphic incompatibility is a stable feature of populations of *Pontederia* species (see Price & Barrett, 1982; Barrett et al., 1983), this is not the case in *Eichhornia*. Only in *E. azurea* do populations occur that possess self-incompatibility, strong pollen trimorphism, and the three style morphs (Barrett, 1978). Even in this species, however, monomorphic populations are common, and genetic modifications favoring self-fertilization occur in Central America. In the remaining tristylous taxa, self-compatibility occurs and is associated with weak heteromorphisms of pollen size. Differences in the degree of pollen heteromorphism among *Eichhornia* species are illustrated in Figure 3. The greatest difference in the mean size of pollen originating from the two anther levels within a flower occurs in the self-incompatible *E. azurea*. Differences are less evident in the two self-compatible tristylous species, *E. crassipes* and *E. paniculata*. In the remaining homostylous species there is evidence of slight differences in pollen size distributions in *E. heterosperma* and *E. diversifolia*, whereas in *E. paradoxa* pollen originating from the two anther levels is uniform in size.

*Self-compatible tristylly.* In the vast majority of heterostylous plants the floral polymorphisms are associated with a sporophytically controlled self-incompatibility system (Ganders, 1979). Absence of such a system in most *Eichhornia* species raises the issue as to whether illegitimate matings are frequent under field conditions and whether the stamen-style polymorphism functioning alone is effective at promoting disassortative mating among the floral morphs. Two studies involving

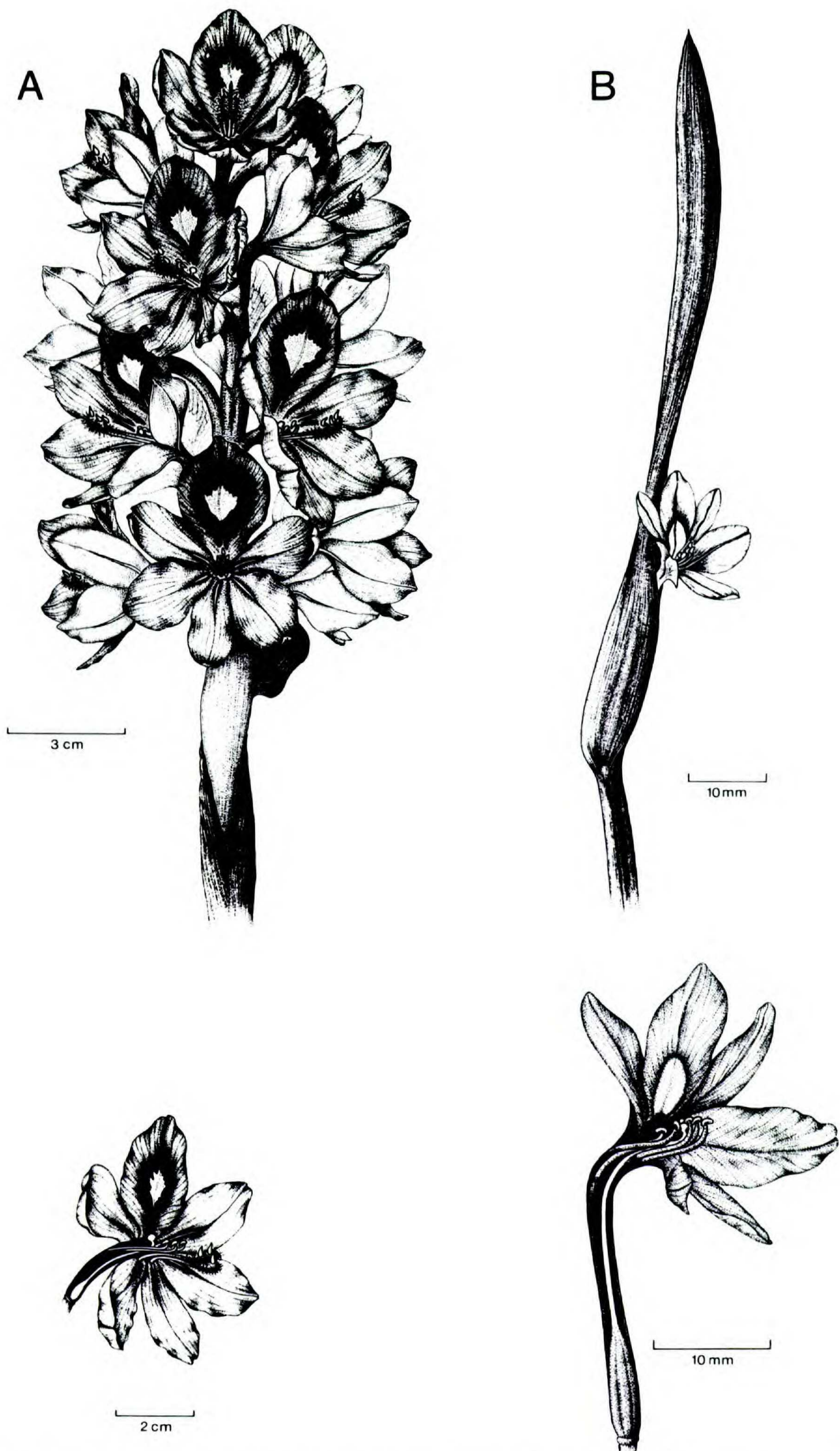


FIGURE 1. Floral displays in a tristylous and a semi-homostylous species of *Eichhornia*.—A. *Eichhornia crassipes*, S morph from Boca de Jari, Lower Amazon, Brazil.—B. *E. paradoxa*, semi-homostylous M morph from Propriá, Sergipe, northeast Brazil.

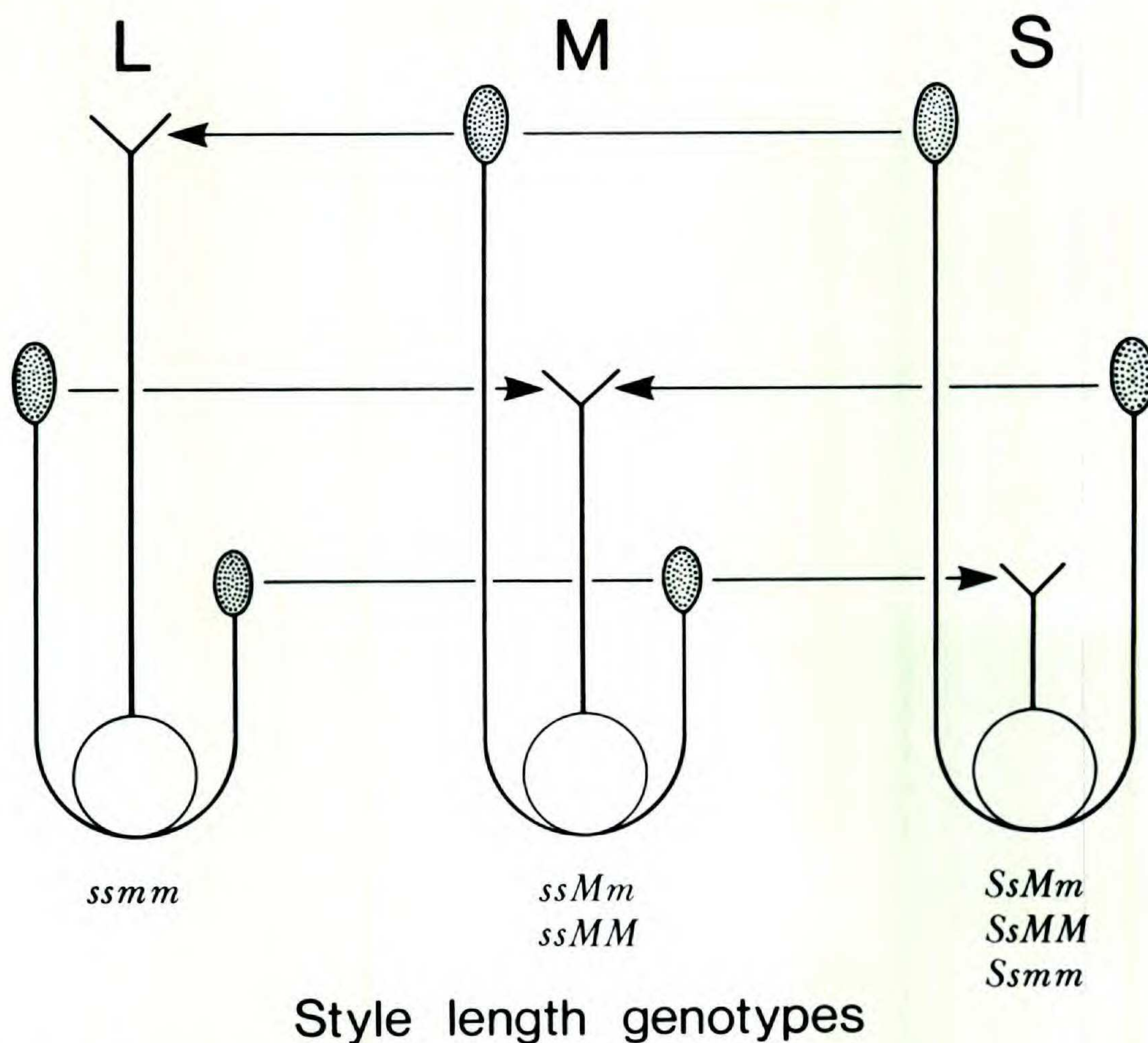


FIGURE 2. Schematic diagram of the relative positions of styles and stamens in the floral morphs of a tristylous species. Legitimate pollinations are indicated by arrows. Genotypes of the floral morphs under the two-locus model (S, M) for the inheritance of tristily in *Eichhornia* are shown.

marker genes indicate that the mating system of floral morphs in self-compatible tristylous populations can involve a high level of outcrossing (Glover & Barrett, 1986a; Barrett et al., 1987). Progeny test data from *E. paniculata* (Table 3) reveal that the floral morphs are largely outcrossing and that most matings are disassortative in nature. This indicates that self and intramorph matings occur infrequently in this population. Such an effect could result from the operation of a cryptic heteromorphic incompatibility system of the type demonstrated in *Amsinckia* (Weller & Ornduff, 1977; Casper et al., 1988). However, this does not appear to be the case. In a controlled pollination experiment on *E. paniculata* that compared the competitive ability of self, illegitimately outcrossed, and legitimately outcrossed pollen, using the *GOT-3* marker locus, Glover & Barrett (1986a) found no evidence of a residual or cryptic trimorphic incompatibility system. Outcrossed progeny were always favored over selfed progeny irrespective of whether they were legitimate or illegitimate.

The results from *E. paniculata* are relevant to the question of whether self-compatibility in tristylous *Eichhornia* species is a derived condition in-

volving relaxation of self-incompatibility. Following this view we might have anticipated some residual influence of the ancestral incompatibility system favoring legitimate over illegitimate matings. However, this was not detected, perhaps because the action of numerous modifier genes has removed all traces of the functional aspects of trimorphic incompatibility. The prepotency of cross-pollen over self-pollen might then be explained as a manifestation of inbreeding depression operating via extensive pollen-pistil interactions and genetically unrelated to the original incompatibility system (Barrett, 1988b).

Comparative evidence from other heterostylous families indicates that self-compatibility is commonly derived from self-incompatibility (Ganders, 1979). Most workers (e.g., Charlesworth & Charlesworth, 1979) have favored the idea that the evolution of self-incompatibility precedes the development of the stamen-style polymorphism in heterostylous groups (although see Richards, 1986).

*Function of tristily.* Although the progeny test data from Recife demonstrate high levels of disassortative mating in *E. paniculata*, this does

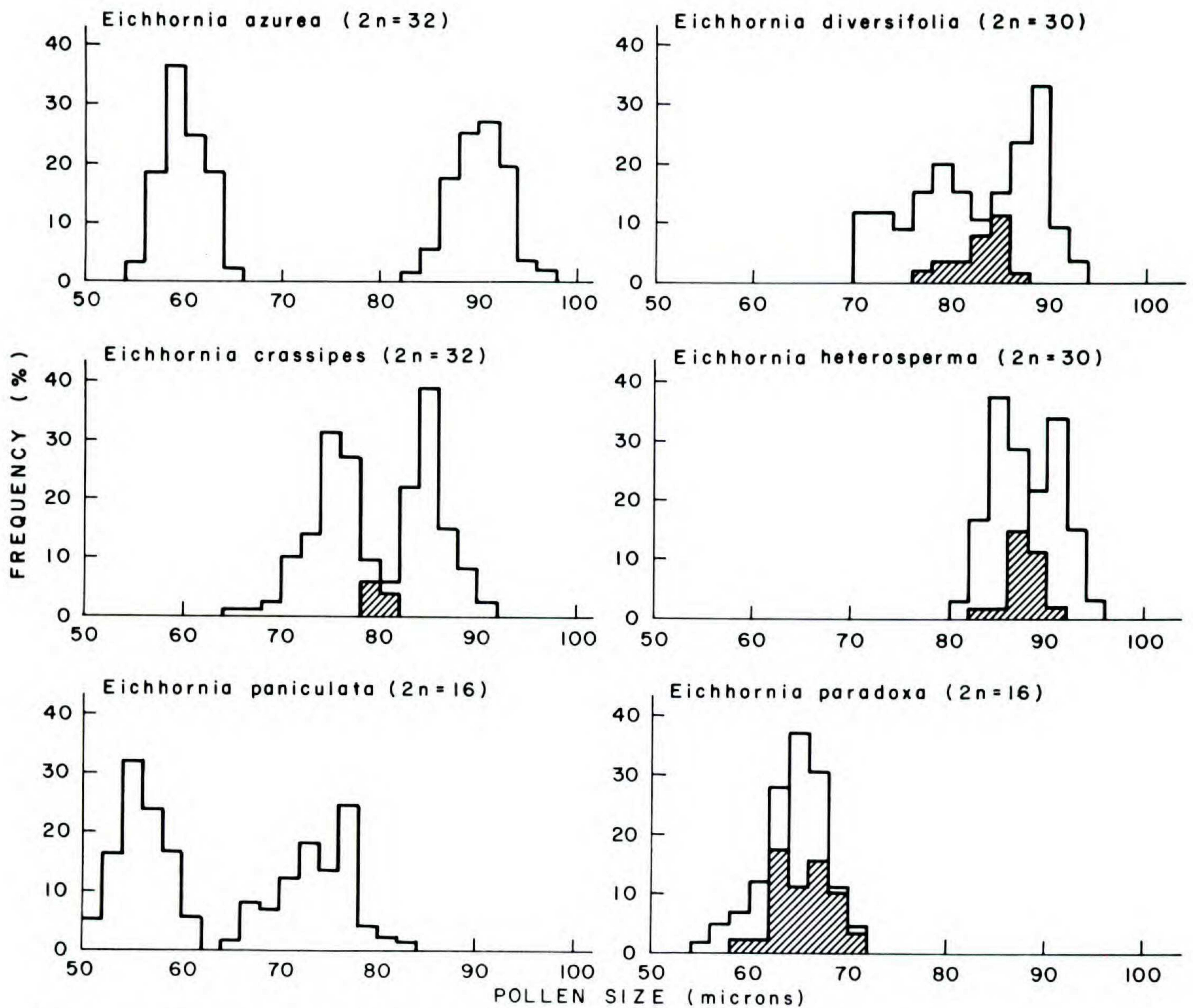


FIGURE 3. Patterns of pollen-size heteromorphism in six species of *Eichhornia* with contrasting breeding systems. The distributions for each species were obtained by measuring the equatorial axis of 200 dry pollen grains originating from the two stamen levels of a flower. To facilitate comparisons among species, all measurements were conducted on the *M* morph (*E. azurea*, *E. crassipes*, *E. paniculata*) or semi-homostylous derivatives of the *M* morph (*E. diversifolia*, *E. heterosperma*, *E. paradoxa*). Note the overall differences in pollen size between diploid and tetraploid species.

not prove that tristylly promotes legitimate pollination, as Darwin (1877) originally proposed. This is because in a self-compatible species intermorph illegitimate matings contribute towards estimates of disassortative mating. Using the progeny test method, it is not possible to distinguish between cross-pollinations involving legitimate and illegitimate pollen that originate from the same plant (Barrett et al., 1987). However, in some heterostylous species, these pollen types differ in size, and it is therefore possible to measure the magnitude of legitimate and illegitimate pollination in natural populations by inspecting the pollen loads of open-pollinated stigmas (Ganders, 1979). The extensive overlap in the size of pollen that originates from different anther levels of self-compatible *Eichhornia* species (Fig. 3) precludes this method. How-

ever, stigmatic pollen loads have been examined in *Pontederia* species, where size trimorphism is well developed, and significant levels of legitimate pollination were recorded in several natural populations (Glover & Barrett, 1983, 1986b; Price & Barrett, 1984; Barrett & Glover, 1985). These studies therefore provide support for the Darwinian hypothesis of the adaptive significance of tristylly.

#### BREAKDOWN OF TRISTYLY

*Disruption of population structure.* For tristylly to function effectively, populations should contain the three floral morphs and provide sufficient pollen and nectar rewards to attract specialized long-tongued pollinators, usually bees. Several influences can disrupt population structure to yield



populations composed of one or two morphs. In *E. crassipes* and *E. azurea*, founder effects and rampant clonal propagation are major disruptive influences on tristylly. This is well illustrated by the geographical distribution of floral morphs in *E. crassipes* (Fig. 4). The S morph is absent from many parts of the New World range as well as from the Old World. In the latter case genotypes of the S morph were not among clones transported to the Old World by man. The M morph predominates in most regions, while the L morph appears sporadically (Barrett, 1977a). In a survey of 196 sites throughout the New World range of *E. crassipes*, Barrett & Forno (1982) found that 77% of the colonies located were monomorphic for style length, 18.4% were dimorphic, and only 4.6% were trimorphic. The rarity of *E. crassipes* populations containing the three floral morphs results from the high dispersal of the free-floating life form coupled with rapid clonal propagation. These factors result in inequalities of representation of founding genotypes. In addition, the short-lived nature of many populations and ecological restrictions on seedling establishment (Barrett, 1980a, b) retard further progress toward isoplethic population structure.

Founder events have also played a disruptive effect on the maintenance of tristylly in *E. paniculata*. Although clonal propagation is absent from this species, repeated colonizing episodes and stochastic influences on population size play a major role in determining morph frequencies in populations. Surveys of population structure in northeast Brazil and Jamaica (Barrett, 1985b and unpubl. data) have revealed a pattern reminiscent of that found in *E. crassipes* (Table 4). The S morph is absent from Jamaica and underrepresented in many populations from Brazil. The M morph predominates in dimorphic populations and, with one exception (see below), is the only morph that has been observed in monomorphic populations.

Absence of the S morph from parts of the range of *E. crassipes* and *E. paniculata* and its underrepresentation in Brazilian populations of *E. paniculata* may be explained by founder events and fluctuations in population size. Since both species are highly self-compatible, polymorphic populations can arise from selfing and segregation of genotypes heterozygous at the S and M loci. However, since the dominant S allele governing the expression of short styles is only carried by the S morph, separate introduction(s) of this morph are necessary for it to become established in a region. In contrast, the m allele can be carried by all three morphs and the M allele by the M and S morphs.

TABLE 3. Estimates of the mating system of floral morphs in a tristylous population (B5) of *Eichhornia paniculata* at Recife, northeast Brazil. Outcrossing rates and levels of disassortative mating were estimated from open-pollinated progeny arrays using six isozyme loci or the two loci governing style length, respectively. After Glover & Barrett (1986a) and Barrett et al. (1987).

Measurement	Floral Morphs		
	L	M	S
Outcrossing rate	0.98	0.97	0.93
N	480	520	480
Standard error	0.021	0.018	0.022
Disassortative mating	0.90	0.93	0.83
N	652	721	665
Standard error	0.034	0.052	0.052

Computer simulation studies by Heuch (1980) on the effects of random fluctuations of population size in tristylous systems confirm that the S morph is most often lost from populations. The same processes, on a neighborhood scale, may also account for the low average frequency of the S morph in trimorphic populations of *E. paniculata* (Table 4). Thus a genetic constraint imposed by the inheritance of tristylly interacting with random ecological processes plays a major role in disrupting the maintenance of population trimorphism.

Disruptions of trimorphic population structure in *Eichhornia* may not necessarily lead to genetic modifications of the breeding system. In *E. azurea* and *E. crassipes*, clonal regeneration and the low frequency of sexual reproduction in many monomorphic and dimorphic populations limit opportunities for evolutionary change. However, under conditions where sexual reproduction is favored, e.g., in strongly seasonal aquatic environments, there may be strong selection pressures to increase fecundity, particularly if pollinating agents are scarce (Barrett, 1979).

*Semi-homostyle formation.* In each of the three tristylous species of *Eichhornia* there is evidence of the breakdown of tristylly and the evolution of semi-homostyly (Barrett, 1978, 1979, 1985a). Semi-homostyles in *Eichhornia* occur primarily at the geographical margins of the neotropical ranges of species either as local populations (*E. azurea*, *E. paniculata*) or as variants in otherwise unmodified population systems (*E. crassipes*). In each species, semi-homostyles are highly autogamous be-

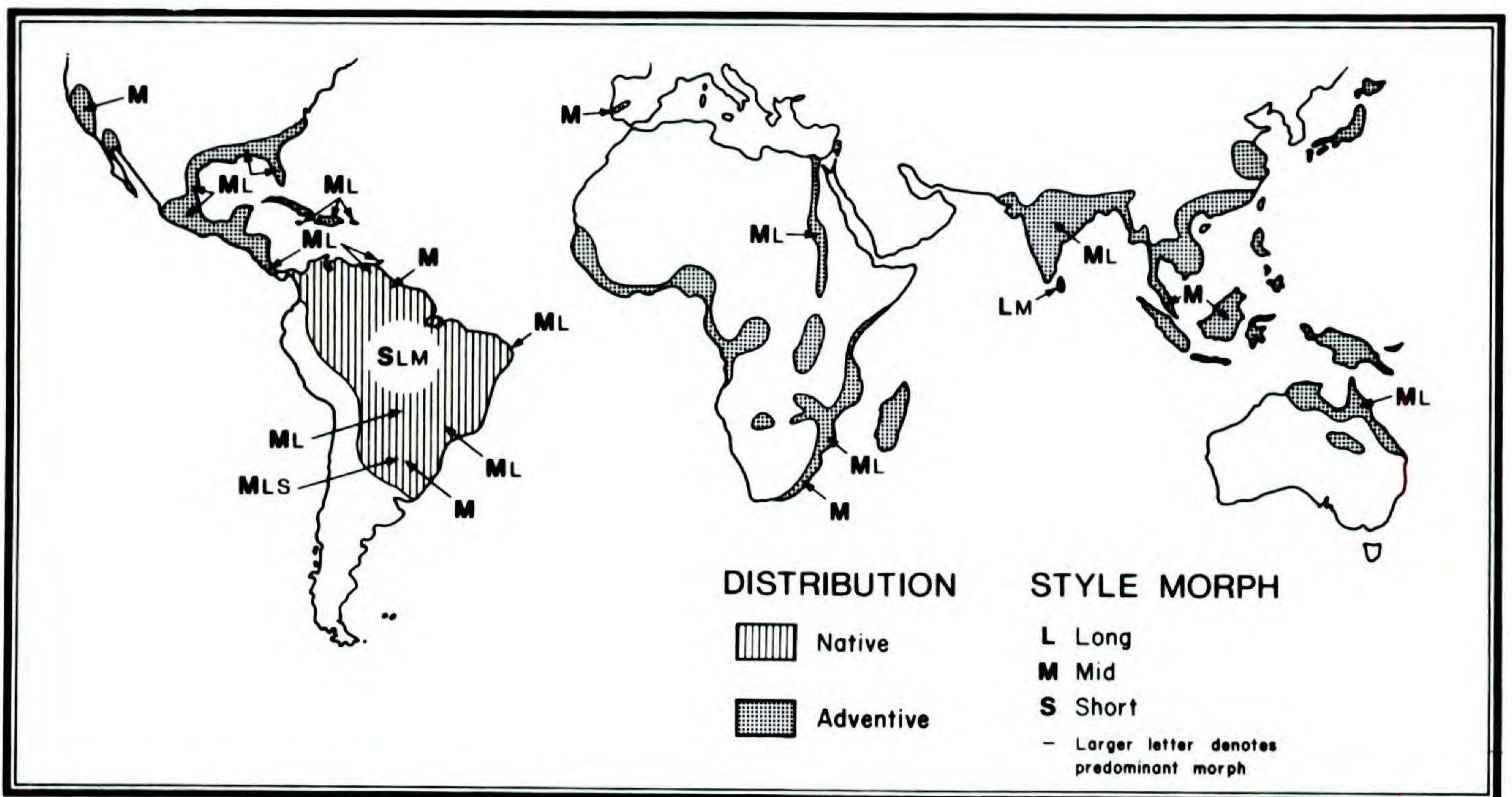


FIGURE 4. The geographical distribution of style morphs in *Eichhornia crassipes*. Modified from Barrett (1977a) and Barrett & Forno (1982).

cause of the close juxtaposition of stigmas and anthers.

In *E. azurea* and *E. paniculata*, semi-homostylous populations differ from their outcrossing progenitors in several floral traits. They often possess smaller, less showy flowers, reduced numbers of flowers per inflorescence, weak pollen heteromorphism, and lower pollen-ovule ratios. As described above, these differences parallel those that distinguish outcrossing and selfing species of *Eichhornia* (Table 2). This point is well illustrated by comparing the degree of pollen heteromorphism displayed by populations of *E. paniculata* with contrasting mating systems (Fig. 5). The difference in size of pollen produced by contrasting stamen levels is large in tristylous populations, whereas dimorphic and monomorphic populations show increasing pollen-size overlap. The weakening of pollen heteromorphism accompanying the evolution of semi-homostyly probably reflects relaxed selection pressures and the random accumulation of small mutations affecting pollen size. These patterns suggest that pollen size is a canalized trait in outcrossing populations and that heteromorphism is maintained by strong stabilizing selection. The functional significance of pollen-size heteromorphism to pollen-pistil interaction in heterostylous species is still a matter of some conjecture (see Ganders, 1979).

Semi-homostylous variants are most common in *E. paniculata*. They predominate in Jamaica and are frequently encountered in dimorphic and mono-

morphic populations in northeast Brazil. In tristylous populations, however, they occur rarely, suggesting some selective disadvantage. The development of semi-homostyly in *E. paniculata* occurs most commonly in the M morph (Fig. 6), with populations displaying various floral modifications in different parts of the range of the species (Barrett, 1985a). This suggests that the breakdown of tristily is occurring repeatedly in the species. Semi-homostylous variants in *E. paniculata* are not exclusively derived from the M morph. Occasionally, modified L plants are encountered in populations from northeast Brazil, and material from

TABLE 4. Average frequencies of the floral morphs in populations of *Eichhornia paniculata* from northeast Brazil and Jamaica. The majority of M plants in non-trimorphic populations exhibit modifications of the short-level stamens (see text).

Region	Number of Populations Sampled	Frequencies		
		L	M	S
Northeast Brazil				
Trimorphic	58	0.374	0.370	0.256
Dimorphic	21	0.336	0.664	—
Monomorphic	5	—	1.00	—
Jamaica				
Dimorphic	7	0.211	0.789	—
Monomorphic	19	—	1.00	—

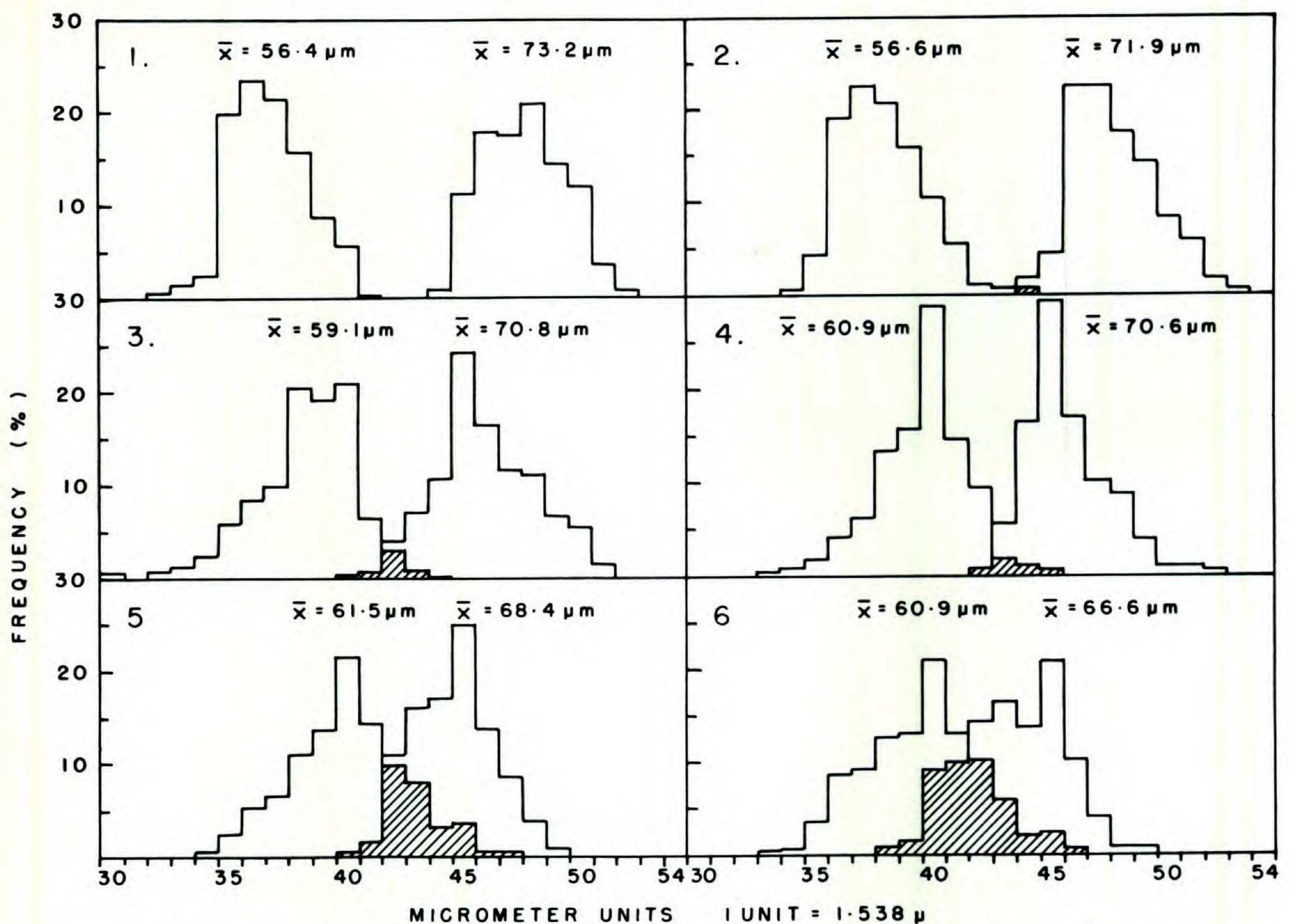


FIGURE 5. Patterns of pollen-size heteromorphism in six populations of *Eichhornia paniculata* with contrasting breeding systems. The distributions for each population were obtained by measuring the equatorial axis of 200 dry pollen grains originating from the two stamen levels of a flower. To facilitate comparisons among populations, all measurements were conducted on six flowers from six plants of the M morph in each population. Plants of the M morph in nontristylous populations possessed varying degrees of genetic modification of the short stamen level (see text for details). Populations 1-4 are from northeast Brazil, populations 5 and 6 are from Jamaica. Populations 1 and 2 are trimorphic, 3 is dimorphic (L, M), and 4-6 are monomorphic (M).

the only reported occurrence of the species in Central America (*Haynes 8442, 8603*, (ALU) Rio Las Lajas, Department of Rivas, Nicaragua) is composed exclusively of semi-homostylous long-styled plants. Ongoing genetic and developmental studies (Richards & Barrett, 1984 and unpubl. data) of the range of semi-homostylous variants in *E. paniculata* are aimed at determining the inheritance patterns and developmental pathways responsible for the breakdown of tristily in the species.

In *E. crassipes* semi-homostyle formation is apparently rare. I have observed semi-homostyles in only two populations. Both were dimorphic (L, M), and in each case the modified phenotypes only differed from unmodified forms in the relative lengths of their reproductive parts (Barrett, 1979 and unpubl. data). If these phenotypes became reproductively isolated from their unmodified progenitors, it is likely that genetic modifications in other aspects of their reproductive biology would occur.

The reported semi-homostyles in a population of *E. crassipes* from Costa Rica are also modified forms of the M morph (Barrett, 1979). However, in contrast to *E. paniculata*, where alterations involve elongation of short-level stamens, the breakdown of herkogamy in this population of *E. crassipes* is primarily the result of shortening of long-level stamens. This indicates that a different developmental pathway is involved. In addition, the recent discovery in *E. crassipes* of a semi-homostylous L morph in northeast Brazil (S. C. H. Barrett, unpubl. data) indicates that, in common with *E. paniculata*, semi-homostyle formation can occur in both M and L morphs.

The arrangement of reproductive organs in semi-homostylous populations of *E. azurea* suggests that they are M variants with elongated short-level stamens (Barrett, 1978 and unpubl. data). Why the M morph of *Eichhornia* species appears to be more prone than other morphs to genetic modifications favoring increased levels of self-fertilization



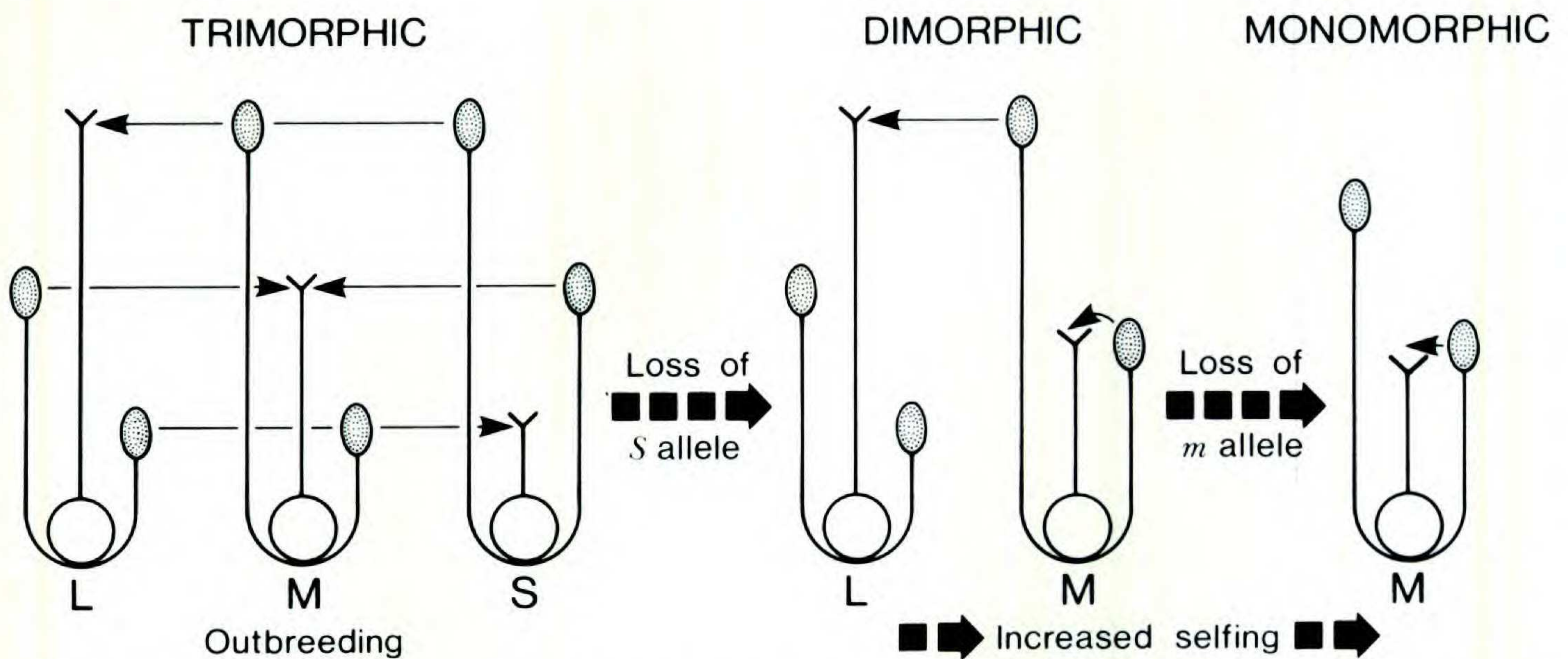


FIGURE 7. Model of the breakdown of tristylty to semi-homostyly in *Eichhornia paniculata*. Arrows indicate predominant matings. Note the modifications in short-stamen position of the M morph in dimorphic and monomorphic populations. After Barrett (1985b).

cycle, and population turnover is rapid due to the unpredictable nature of its habitats. These features increase the likelihood of detecting microevolutionary changes. This situation contrasts with that in *E. azurea* and *E. crassipes* where, because of heavy emphasis on clonal propagation, evolutionary changes in the breeding system of populations are more difficult to measure.

*The breakdown process in Eichhornia paniculata.* Surveys of the patterns of floral-morph frequency in populations of *E. paniculata* in conjunction with studies of their reproductive ecology and genetics have enabled the formulation of a model of the breakdown process (Barrett, 1985b; Glover & Barrett, 1986a, 1987). Figure 7 illustrates the major stages in the breakdown of tristylty to semi-homostyly in the M morph of *E. paniculata*. The model emphasizes two key stages: loss of the S allele and hence the S morph, and second, loss of the m allele and thus the L morph. Stochastic influences on population size, as discussed above, are thought to be largely responsible for the disappearance of the S morph from populations. However, because of its concealed stigma, a loss of specialized long-tongued pollinators in small populations may also reduce the maternal fitness of the S morph and hence its representation in founding populations. Comparisons of the fecundity of floral morphs in populations serviced by either long-tongued bees (*Florilegus festivus* and *Ancyloscelis* spp.) or generalist bees (*Trigona* spp. and *Apis mellifera*) provide evidence in support of this suggestion (S. C. H. Barrett, unpubl. data).

Loss of the L morph and fixation of the M morph

in populations of *E. paniculata* are associated with the spread of mating system modifier genes and the evolution of semihomostyly. The genes that modify the short-level stamens of the M morph have no significant phenotypic effects when carried by the L and S morphs. As a result, in dimorphic populations, plants of the M morph frequently display altered stamen positions, whereas the L morph remains unmodified (e.g., fig. 3 in Glover & Barrett, 1986a, and Fig. 6). This pattern is also evident in *E. crassipes* (e.g., fig. 2 in Barrett, 1979). This phenotypic difference between the floral morphs of *E. paniculata* has a profound effect on their mating systems. Unlike tristylous populations where each morph is highly outcrossed, in dimorphic populations the M morph often experiences a high level of self-fertilization, whereas the L morph remains largely outcrossing (Glover & Barrett, 1986a; Barrett et al., 1987; Barrett, 1988a). With this mating asymmetry, and no major fitness differences between progeny arising from them, the M morph will likely replace the L morph. This is because the genes that cause an increased rate of self-fertilization have an "automatic advantage," since the maternal parent will transmit genes via both pollen and ovules to selfed progeny and thus evade the "cost of meiosis" (Maynard Smith, 1978).

An additional advantage that modified M plants possess over other floral morphs is their facility for automatic self-pollination in the absence of pollinating agents. Frequent colonizing episodes resulting in periods of low density are more likely to favor establishment of semi-homostylous variants, and this likely accounts for the predominance of populations monomorphic for the M morph in Ja-

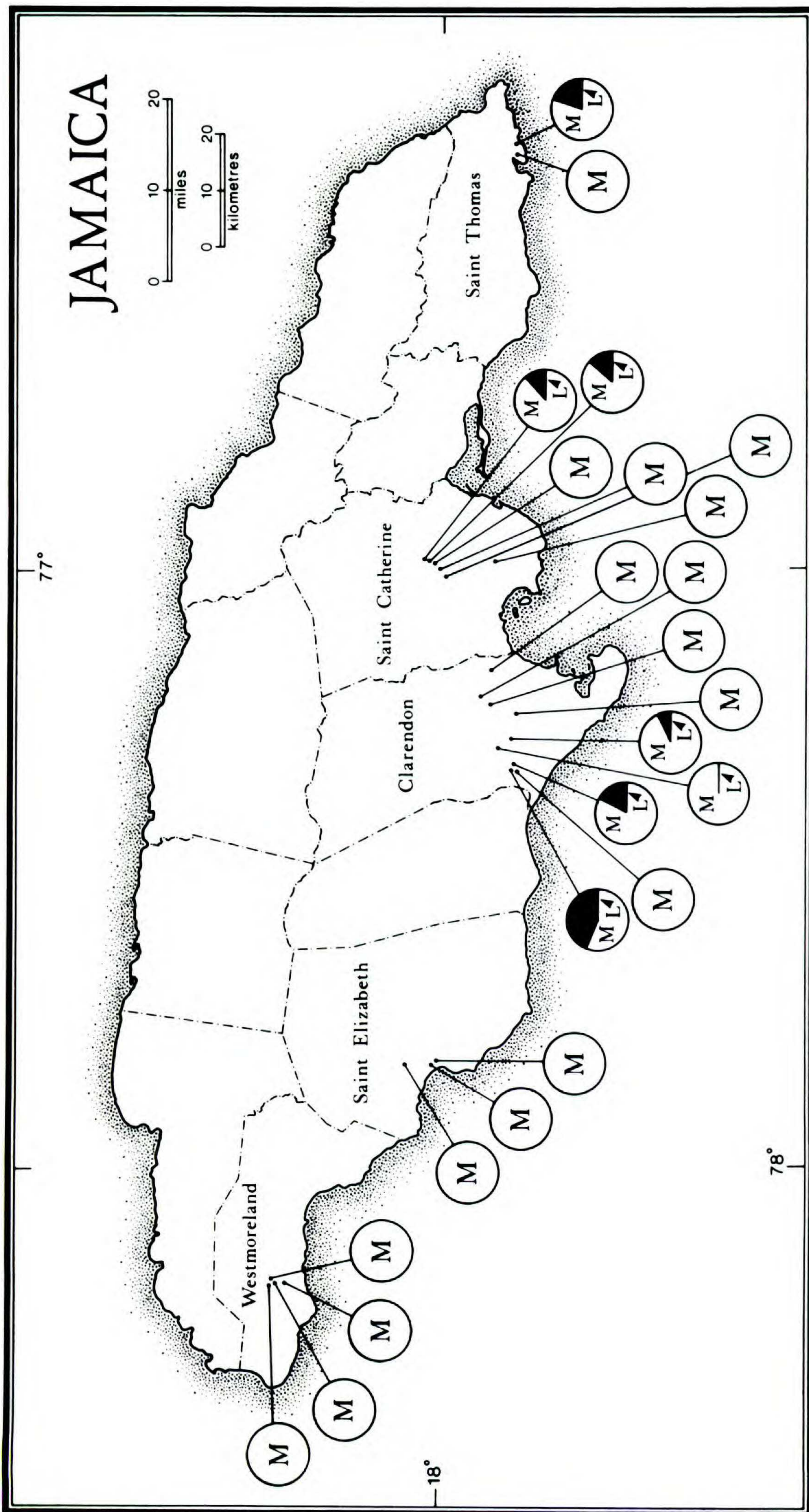


FIGURE 8. Pattern of style-morph distribution in *Eichhornia paniculata* populations from Jamaica. Surveys were conducted in January 1979, 1984, and 1987. All plants of the M morph in Jamaica exhibit modified short-level stamens and are highly autogamous.

maica (Fig. 8). The fecundity advantage of semi-homostylous variants of the M morph over the L morph has been demonstrated in Jamaican populations of *E. paniculata* (Barrett, 1988a) as well as in a dimorphic (L, M) population of *E. crassipes* (Barrett, 1979). The reproductive assurance of homostyly under conditions of low density and uncertain pollinator service has been used to explain the geographic patterns of floral variation in several other heterostylous groups (Baker, 1953, 1959; Ganders, 1975; Barrett & Shore, 1987).

#### FLORAL HETEROMORPHISMS IN SELFING TAXA

A second source of evidence in support of the derived nature of selfing in *Eichhornia* comes from investigation of the patterns of variation in floral traits within and among populations of predominantly autogamous taxa. As we have seen, in monomorphic and dimorphic populations of *E. paniculata*, residual floral heteromorphisms that were originally components of the ancestral tristylous syndrome remain in populations despite their largely selfed mating systems. Although the expression of these traits may be considerably modified from their original form, their occurrence in selfing species of *Eichhornia* is direct evidence that these taxa are descended from tristylous ancestors via evolutionary breakdown of tristily.

*Intrapopulation variation.* Over most of the range of *E. heterosperma* and *E. diversifolia*, populations are composed of a single floral phenotype with a mid-length style and one set of anthers positioned just above the stigma and another below (Figs. 9 and 10, respectively). Because flower size is reduced in both species, the distance separating the reproductive organ levels is often small. In some populations this makes it difficult to determine the homologous positions of an ancestral tristylous condition and thereby infer the morphs from which the phenotypes descended. In most populations the phenotypes are best interpreted as semi-homostylous M plants in which elongation of the short stamen level into the mid position has occurred. Although this origin seems most plausible, based on analogy with semi-homostyle formation in outcrossing *Eichhornia* species, the possibility that some phenotypes are modified S plants with elongated styles cannot be ruled out.

Field studies of *E. heterosperma* in Venezuela and *E. diversifolia* in northeast Brazil have revealed a different pattern of floral variation. In both species a second floral phenotype can be found in populations in addition to the phenotype de-

scribed above. The two phenotypes differ in style length, style coloration, pollen size, and the relative positions of their reproductive parts (Table 5). The expression of traits in the second phenotype indicates that it is a semi-homostyle derived from the L morph. The two semi-homostyles in *E. diversifolia* are illustrated in Figure 10. A trait of particular value in determining the origin of these floral phenotypes is style coloration. In tristylous *Eichhornia* species the three floral morphs differ in the degree of pigmentation of their styles. For example, in *E. crassipes* the L morph has a purple style, the M morph a lavender style, and the S morph a white style (Barrett, 1977a). In *E. diversifolia* and *E. heterosperma* the styles of the two semi-homostyles are pigmented to different degrees with the semi-homostylous L phenotype being either purple (*E. diversifolia*) or pink (*E. heterosperma*) and the semi-homostylous M phenotype light pink or white. In *E. heterosperma*, the two morphs can also differ in perianth color, with the semi-homostylous L phenotype possessing dark blue tepals and the M phenotype pale blue tepals. Differences in perianth color among the floral morphs of *Eichhornia crassipes* have also been reported, although this is not a universal feature of the species throughout its range (Müller, 1883; Haigh, 1936; Barrett, 1977a).

Populations of *E. diversifolia* and *E. heterosperma* that contain the two semi-homostylous phenotypes are largely self-pollinating, and it seems unlikely that the residual polymorphisms have any functional significance. If this is true, we might expect that mutation pressure will eventually break down the discontinuities that currently exist between the forms. Further field studies are required, however, to establish the overall distribution patterns of the morphs and to determine whether fitness differences that relate to floral phenotype exist. A recent survey of *E. diversifolia* populations in Ceará, northeast Brazil, provided no evidence that the two semi-homostylous phenotypes exhibit nonrandom distributions (S. C. H. Barrett, unpubl. data).

The rarity of *E. paradoxa* has restricted our investigations of its floral biology to surveys of herbarium specimens and to experimental studies of two natural populations from Paraiba and Sergipe, northeast Brazil. Even in this small sample several distinct patterns have emerged. The two field populations were each composed of a uniform but different self-pollinating semi-homostylous phenotype. One of these is illustrated in Figure 1B. The arrangement of reproductive parts and style coloration in the phenotypes is similar to the two semi-homostylous forms described above. It there-

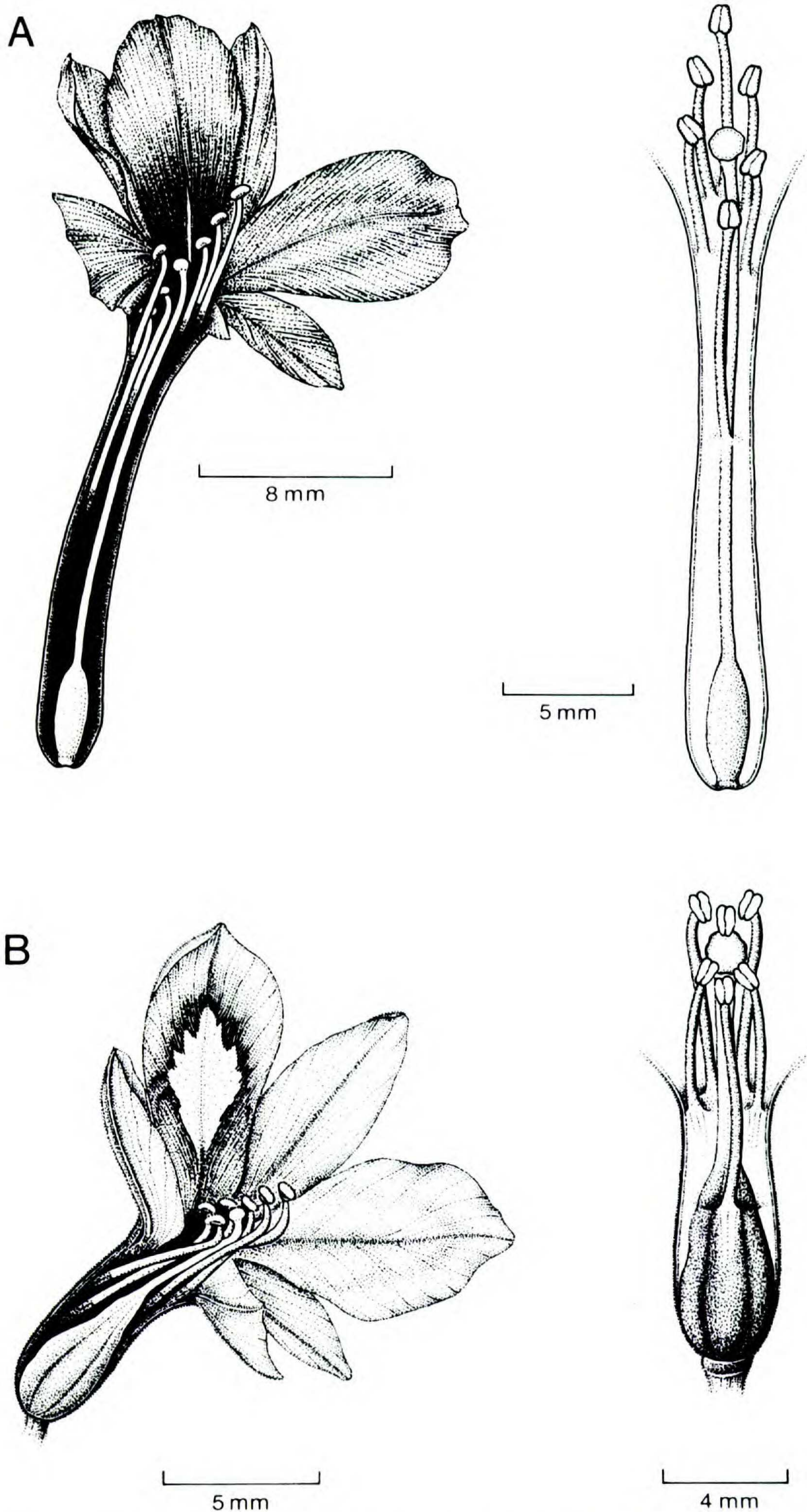


FIGURE 9. Flowers and reproductive organs of semi-homostylous species of *Eichhornia*.—A. *E. heterosperma* (from Ceará, northeast Brazil).—B. *E. meyeri* (from Nueva Asunción, Paraguay). Note the close proximity of stigmas and anthers in the two species. A second floral phenotype occurs in parts of the range of *E. heterosperma* (see text).



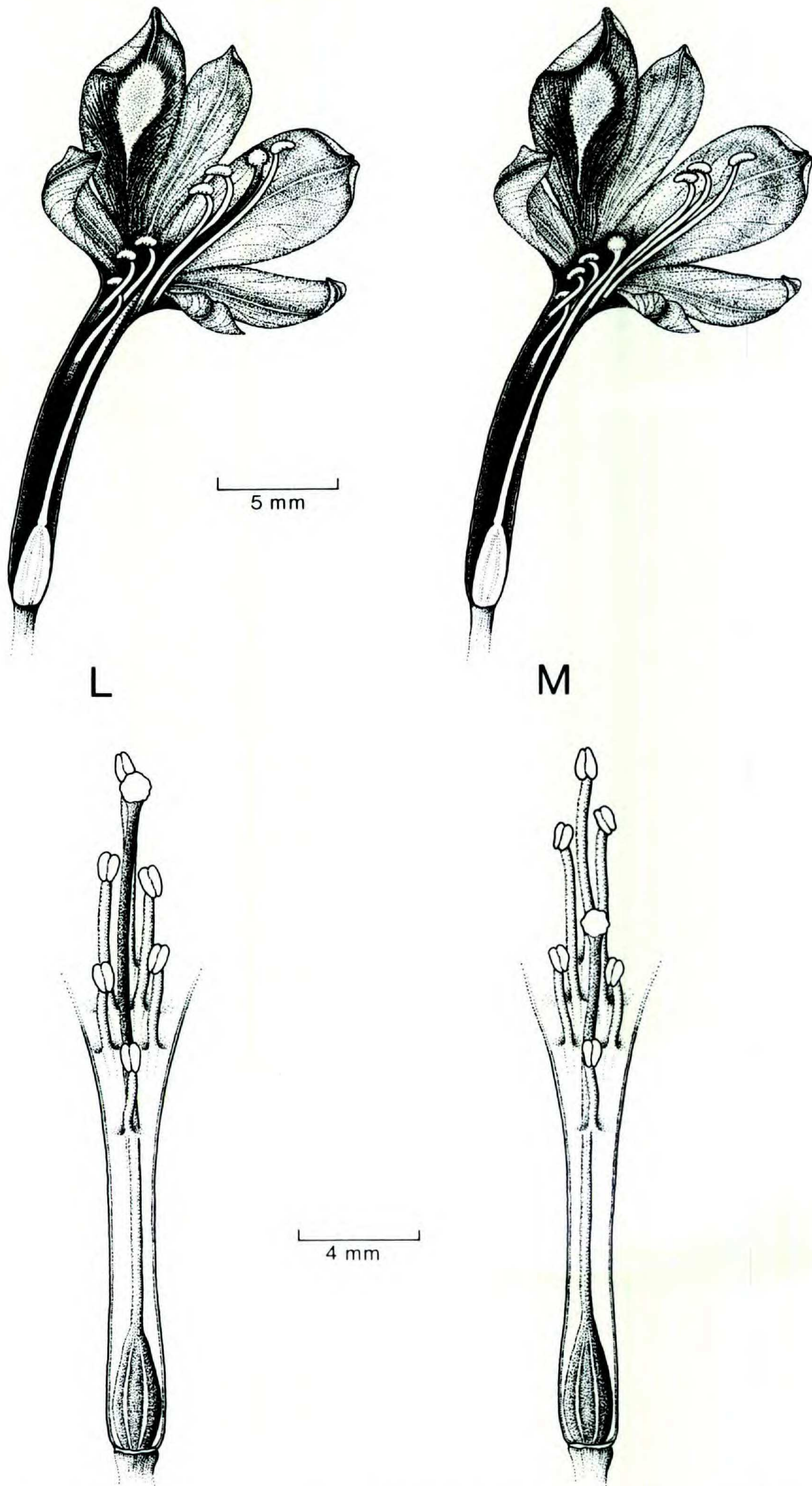


FIGURE 10. Semi-homostylous L and M morphs of *Eichhornia diversifolia* from a population in Ceará, northeast Brazil. Note the differences in style length and pigmentation in the floral morphs.

TABLE 5. Mean style lengths and stamen heights (in mm) in semi-homostylous morphs of *Eichhornia diversifolia* and *E. heterosperma*. Measurements were made on field-collected flowers from populations at Croata, Ceará, northeast Brazil ( $N = 24$  flowers per morph) and Calobocho, Guárico, Venezuela ( $N = 10$  flowers per morph), respectively.

Trait	<i>E. diversifolia</i>		<i>E. heterosperma</i>	
	Semi-homostylous L	Semi-homostylous M	Semi-homostylous L	Semi-homostylous M
Mean style length	26.3 ± 0.8	*** 21.1 ± 0.9	23.7 ± 0.7	** 22.8 ± 0.6
Mean height of upper stamens	24.1 ± 0.9	*** 25.8 ± 1.2	22.4 ± 0.7	*** 24.1 ± 0.7
Mean height of lower stamens	18.4 ± 0.8	ns 18.8 ± 1.2	17.7 ± 0.8	*** 20.0 ± 0.8

\*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , ns = not significant following Student's  $t$ -tests.

fore seems reasonable to assume that they are semi-homostylous L and M morphs. This can be confirmed by controlled crosses between the phenotypes, followed by genetic analysis of  $F_1$  and  $F_2$  variation.

Herbarium collections of *E. paradoxa* from a population in Bahia (Harley 21401 (K), Bahia, Brazil) appear to contain three floral phenotypes that correspond to the L, M, and S morphs of a tristylous system. These plants possess inflorescences that contain many large flowers, and it is possible that the population retains a functionally tristylous breeding system. If this is true, *E. paradoxa* would resemble *E. azurea* and *E. paniculata* in displaying both outcrossing and selfing population systems. Because of its rarity and markedly disjunct distribution, it is probable that the species possesses considerable interpopulation differentiation, with individual populations displaying different stages in the breakdown of tristylous. Further studies of this interesting taxon are planned.

**Floral monomorphism.** Studies of the remaining two *Eichhornia* species (*E. natans* and *E. meyeri*) have as yet provided no evidence of polymorphisms in floral traits associated with the heterostylous syndrome. Both species exhibit mid-length styles and two stamen levels positioned very close to the stigma, one above and one below (Fig. 9B for *E. meyeri*). *Eichhornia natans* has highly reduced uniform blue flowers, and it is possible that the species is "quasi-homostylous" rather than semi-homostylous (see Ornduff, 1972). In quasi-homostyly the close juxtaposition of anthers and stigmas results from the reduced size of flowers rather than from genetic modifications in the relative positions of reproductive parts. Glasshouse studies of *E. meyeri* material collected from Paraguay (Billiet & Jadin 3211 (BR), Nueva Asunción, Paraguay) indicate that the species is self-compatible, highly autogamous, and without residual pollen-size heteromorphism. The flowers

of this collection are illustrated in Figure 9. Further work on both species is required to establish firmly the relationships of their breeding systems to an ancestral tristylous condition. This may be difficult if both species have lost all of the polymorphic variation associated with the tristylous syndrome. In *E. natans* this could have occurred through a genetic bottleneck during dispersal and establishment on the African continent. In *E. meyeri* progressive extinctions leading to its current rarity may have had a similar effect.

#### CONCLUSIONS

Studies of intraspecific and interspecific patterns of variation in the breeding systems of *Eichhornia* species indicate that tristylous has broken down repeatedly in the genus to give rise to predominantly selfing population systems. This conclusion rests on two lines of evidence: 1) the evolution of semi-homostylous forms within each of the three primarily tristylous species (*E. azurea*, *E. crassipes*, *E. paniculata*), and 2) the occurrence of residual floral heteromorphisms in several of the largely autogamous semi-homostylous species (*E. diversifolia*, *E. heterosperma*, *E. paradoxa*). The pathway of evolution from outcrossing to selfing in *Eichhornia* appears to be the only major shift in breeding system in the genus. This contrasts with the Lythraceae and Oxalidaceae, where, in addition to semi-homostyle formation, stable distylous breeding systems have evolved from tristylous (Mulcahy, 1964; Ornduff, 1972; Lewis & Rao, 1971; Weller, 1976; Charlesworth, 1979).

The selective pressures responsible for the change from outbreeding to inbreeding are always difficult to identify (Jain, 1976); however, ecological and genetic studies of *Eichhornia* populations have provided some insights into the conditions that foster the breakdown of tristylous. Genetic bottlenecks resulting from long-distance dispersal, as well as colonization of unpredictable habitats with uncer-

tain moisture regimes play major roles in disrupting the maintenance of tristylly. Two features of *Eichhornia* species make them particularly prone to these effects: 1) their small-seeded habit favoring bird dispersal, and 2) their occurrence in tropical aquatic habitats that are susceptible to frequent droughts. These aspects of *Eichhornia* ecology result in frequent colonizing episodes and periodic fluctuations in population size. Under these influences, ecological and genetic conditions are likely to favor the establishment and spread of selfing genotypes. In small newly founded populations, serviced by unreliable generalist pollinators, semi-homostylous variants are likely to be at a selective advantage because of the reproductive assurance that autonomous self-pollination provides. In addition, the genetic load of populations may be sufficiently low, owing to frequent bottlenecks (see Lande & Schemske, 1985), that inbreeding depression may not be a serious obstacle to the spread of semi-homostylous variants.

Our discussion of the breakdown of tristylly in *Eichhornia* has focused primarily on details of the ecology and genetics of natural populations. However, for a comprehensive model of the breakdown process to be obtained, information from morphology and development needs to be integrated with studies from population biology. This is of particular importance in heterostylous groups, because the floral morphs can respond differently to selection and drift as a result of their particular floral morphologies and inheritance patterns. While in *Eichhornia* mutations affecting floral structure and mating system can arise in each morph, the available evidence indicates that the M morph is more susceptible to evolutionary modification. This may be because developmental constraints restrict the range of floral modifications that can occur in the L and S morphs. In addition, the S morph is frequently lost from populations through stochastic processes and may rarely encounter the selection pressures operating in small populations that favor the evolution of self-fertilization. Thus loss of the S morph may simply reflect a genetic constraint imposed by the two-locus system of inheritance of tristylly. While frequent colonizing episodes and ecological radiations into temporary aquatic habitats appear to be the major driving forces responsible for the evolution of breeding systems in *Eichhornia*, constraints imposed by the morphology and genetics of the polymorphism have guided the nature of the floral modifications that have occurred.

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